

NATURAL HISTORY OF LEAF-FOLDING CATERPILLARS,
DICHOMERIS SPP. (GELECHIIDAE), ON
GOLDENRODS AND ASTERS

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Abstract.—Ten species of caterpillars in the genus *Dichomeris* were collected on *Solidago* and *Aster* spp. in the northeastern U.S.; an eleventh species was collected on *Solidago* in Florida. New host records are presented. Most species fly in summer and overwinter as partly grown larvae. Some species are restricted to open habitats; others occur in both forest and field. Larvae can be distinguished by color pattern. All but one of the species are leaf folders; some species fold leaves tightly and others loosely. Overall forms of leaf folds vary among host plant species, reflecting differences in position of natural bends in the leaves which larvae always choose as starting points for leaf folds. Ovipositing adults *D. leuconotella* and *D. ochripalpella* prefer tall ramets, so that eggs and summer-hatching larvae are concentrated on the tallest host plant species (*S. altissima*). Partly grown caterpillars redistribute themselves more evenly among host species in the following spring. Adults of at least four species avoid ovipositing on *S. caesia*, although *S. caesia* is much used by the single apparently spring-hatching species, *D. bilobella*. Parasitoids are shared among the summer-hatching caterpillar species; *D. bilobella* is attacked by a different set of parasitoids.

Caterpillars in the large genus *Dichomeris* (Gelechiidae) often feed on composites, particularly *Solidago* and *Aster* species. Hodges (1986) listed 12 North American *Dichomeris* species that had been reared from *Solidago* and/or *Aster* species, ten of which occur in the northeastern United States. In New York State, *Dichomeris* is by far the most diverse of the lepidopteran genera recorded on *Solidago* (Forbes, 1923, 1948, 1954, 1960; R. B. Root, C. C. Loeffler, and J. E. Rawlins, unpubl.). The caterpillars of most of the species are leaf folders.

This paper presents data from six years of collections, rearings, and behavioral observations of *Dichomeris* species, primarily on *Solidago* spp. but also on the closely related species *Euthamia graminifolia* (L.) and on *Aster* spp. Included are many new or more specific host plants records as well as records of two *Dichomeris* species whose caterpillars were previously unknown. Also included are data on relative abundances, habitat distributions, phenology, and behavior of the various species' caterpillars, as well as notes on adult biology and behavior and on identities and relative abundances of the species' parasitoids.

METHODS

Field collections, rearings, and identifications. From 1983 to 1988, I collected and reared *Dichomeris* caterpillars from goldenrods and asters in a variety of habitats

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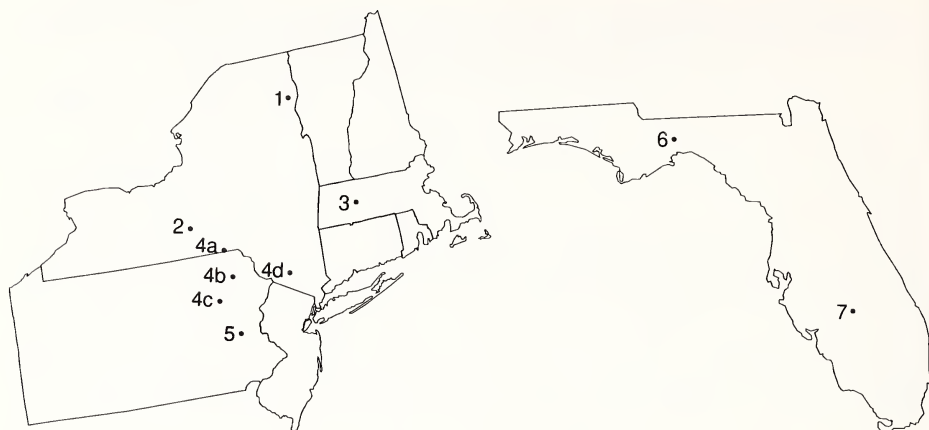


Fig. 1. Locations of collections of *Dichomeris* species: 1. Essex County, New York: several fields, forest openings, and forests. July–August, 1983–1991. 2. Tompkins, Tioga, Cayuga, Seneca, Schuyler, and Cortland Counties, New York: Forty-three sites, in a variety of habitats as shown in the local map in Figure 2. Mostly in April–October, 1983–1988. 3. Hampshire County, Massachusetts: several sites along forest edges and in roadside fields. Late April, 1985 and 1988. 4. Orange and Broome Counties, New York, and Lackawanna and Luzerne Counties, Pennsylvania: fields along Interstates 84 and 81. Late April–May or June, 1983–1988. 5. Berks, Lehigh, Carbon, and Schuylkill Counties, Pennsylvania. Several large fields, forests, and fields succeeding to forest. April–Oct, 1983–1984 and early May, 1985. 6. Leon County, Florida: large fields, Tall Timbers Research Station, Tallahassee. April 1984. 7. Highlands County, Florida. Open scrub, Archbold Biological Station, Lake Placid. March–April 1984.

and geographic locations (Figs. 1, 2). In 1983, to establish caterpillar species presences in oldfields, I examined 15–25 ramets each of the five most abundant field goldenrod species, *Solidago altissima* L., *S. rugosa* Ait., *S. juncea* Ait., *S. gigantea* Ait., and *Euthamia graminifolia*, in four fields in areas a, b, and c of Figure 2 (Cayuga Lake Basin of Central New York). During these samples, conducted every 1–2 weeks from late May to mid September, I searched all aboveground portions of each ramet and collected all caterpillars on the ramets for rearing and identification.

In 1984, seeking comparative data for forests and fields, I took regular samples of 50 ramets each of *S. altissima* and *S. rugosa* in an oldfield and 50 ramets each of *S. rugosa* and *S. caesia* L. in adjacent upland forest in area c of Figure 2. I took similar sample in an oldfield and an adjacent swampy forest in area b (Fig. 2), but I substituted *Aster lateriflorus* L. for *S. caesia* which was scarcer at that locality. I took these samples at 10–15 day intervals from early May to late September.

Additional, informal collections were taken from any species of goldenrod or aster encountered in the various sites in Figures 1 and 2. Some larvae were collected during annual June and September surveys of the fauna of *S. altissima* in 22 oldfield sites scattered throughout the Cayuga Lake Basin. (Data from these surveys are presented in Root and Cappuccino, 1992.) I took large spring collections from fields and forests in areas a–c (Fig. 2), which supplied most of the captive breeding stock. Finally,

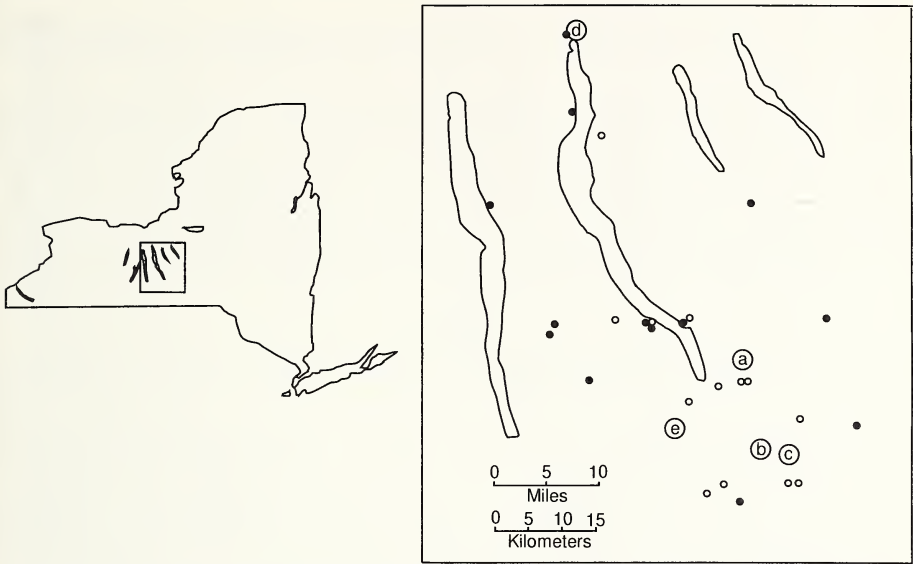


Fig. 2. Locations of the 43 sampling sites in the Cayuga Lake Basin and surrounding area of central New York. Lettered circles represent intensively sampled areas, as indicated in Methods. Closed circles represent oldfield sites sampled in June and September. Open circles represent irregularly-sampled forests, forest edges, streambanks, gravel bars, or beaver meadows.

smaller collections were made at various times from April to October in natural or semi-natural forest openings (small clearings, beaver meadows, streambanks, and gravel bars) and in additional forest and field sites. Some sites were visited specifically because they harbored an unusual goldenrod or aster species.

Gravel bars were of special interest because they may have been strongholds of "field" goldenrod species before European settlement (Marks, 1983), yet they may be inhospitable sites for most *Dichomeris* species whose caterpillars overwinter in the ground litter. To determine whether overwintering was possible in such sites, I augmented natural populations of young larvae on two gravel bars in October, 1984 (for details of methods used see Loeffler, 1992). I revisited the bars to collect surviving larvae in May, 1985.

Rearing methods are described in Loeffler (1992). Briefly, caterpillars were generally reared individually in glass scintillation vials or in small groups in plastic boxes, on excised leaves of *S. altissima* or other available host species. Rearings in 1985 occurred outdoors, in an open barn. Also, over four hundred caterpillars, mostly of *D. leuconotella* (Busck) and *D. bilobella* (Zeller), were monitored on live plants in field or forest, often in cages (dacron sleeves tied over the plants). Phenological information in this paper is based on field observations and outdoor rearings.

Dichomeris adults were identified by R. W. Hodges, J. E. Rawlins, and me. Parasitoids were identified by J. E. O'Hara (tachinids) and by the following research entomologists at the U.S. National Museum: P. M. Marsh (Braconidae), M. E. Schauff

(Eulophidae, Encyrtidae), and R. W. Carlson (Ichneumonidae). Voucher specimens are deposited in the U.S.N.M. and in the Cornell University Insect Collection under Lot No. 1209.

Observations and manipulations to examine larval biologies. I followed several hundred *Dichomeris* larvae of the different species through part or all of their development, on a variety of *Solidago* and *Aster* species. Captive breeding colonies allowed study of newly hatched larvae of several species. To study the life history of *D. bilobella*, whose young larvae were curiously absent in the field when those of other species were appearing in late summer, required a different protocol. I caged many *D. bilobella* adults on several species of goldenrods and asters in summer and examined the potted plants for larvae through late summer and autumn. I then covered the pots and their senesced ramets with muslin and overwintered them outdoors, keeping the soil in the pots slightly moist. In spring I monitored the new ramets for larvae.

Overwintering biology of summer-hatching species was studied in several ways. I reared larvae of several species indoors to determine requirements for winter dormancy. To follow larval movements to and from winter refuges, I took Tulgren funnel extractions of leaf litter from the ground and from standing ramets, at various times in fall and spring. I also monitored captive individuals overwintered outdoors in containers of leaf litter, and I observed their behavior on emergence from overwintering refuges in spring. One set of trials addressed how far larvae wander from their autumnal host: I introduced early instar *D. flavocostella* (Clemens) and *D. leuconotella* larvae (about 45 of each species) to clumps of *S. altissima* ramets growing outdoors in the center of four 60 × 60 cm wooden boxes in October 1984 and trapped them from surrounding leaf litter in the following spring before new *S. altissima* ramets began to appear aboveground. Trapping was accomplished by collecting leaf litter from various zones in the boxes—0.5 cm, 5–30 cm, and >30 cm from the dead plant ramets—and placing the leaf litter from each zone in a separate large dishpan indoors in which there already grew many new *S. altissima* ramets. I examined these plants every day or two thereafter for larvae emerging from the litter.

Adult behavior and host plant preference. I bred adult moths in insect cages or in large plastic rearing boxes. Water and either cut fruit or a solution of honey and water was provided every 1–2 days (the liquids via soaked paper tissues). For oviposition, I added cut host plant ramets (with their bases in vials or jars of water) or potted host plants. I made informal observations of the moths' feeding and mating behavior at various times of day and night.

To study adult host plant choice in *D. leuconotella*, *D. flavocostella*, *D. ochripalpella* (Zeller), and *D. levisella* (Fyles), I set up cages each containing one 15 cm ramet top of *S. rugosa* collected in oldfield, one 15 cm ramet top of *S. rugosa* collected in forest, and two 25 cm ramet tops of the strictly forest species *S. caesia*. I presented an excess of *S. caesia* as a conservative measure, because 1984 observations using potted plants suggested that it was not favored as a host. I placed ramet tops in uniform-sized jars of water, inserted through a perforation in the lid, and caged several male and female moths with each group of plants for four–five days. Numbers of eggs laid on the three types of goldenrods were compared with a Quade test (Conover, 1980), or with a G test (using Williams' correction, Sokal and Rohlf, 1981) for species with four or fewer trials. G tests required the assumption that each egg represented independent laying

events, which was probably generally the case; but egg distributions suggested that moths occasionally "dribbled" two or more eggs in rapid succession.

Similar oviposition trials addressed why young, later summer *Dichomeris* larvae are more numerous on *S. altissima* than on the other common field species, *S. rugosa* (Fig. 9). Preference for *S. altissima* could result simply from its greater height. To test this possibility, I set up cages each with tall (28 cm) and short (14 cm) ramet tops of *S. altissima* and *S. rugosa* arranged in a Latin square design (16 ramets per cage). Numbers of eggs laid over several days were analyzed using a Quade test (*D. leuconotella*, 12 trials) or a goodness of fit G test (*D. ochripalpella*, four trials).

RESULTS

Distributions, relative abundance, and host plants. I collected 11 species of *Dichomeris* from *Solidago* spp., *Euthamia graminifolia*, and *Aster* spp.: 10 in the Northeast and two of these plus an additional species in Florida (Table 1, Fig. 1). The 11 species included nine previously reared by lepidopterists from *Solidago* and/or *Aster*, and two (*D. purpureofusca* and *D. achne*) whose caterpillars were previously unknown (Hodges, 1986). Three other North American *Dichomeris* species have been reared from these host genera by previous workers. One of these, *D. copa* Hodges, occurs in the northeastern U.S. and Canada; the only rearing record was from *Solidago* in Nova Scotia (Hodges, 1986). Its absence from my collections implied local rarity, at least on *Solidago*. The other two are a western species and a species known only from Kentucky (Hodges, 1986).

Five of the species were sufficiently common that I was able to document habitat distribution patterns. *Dichomeris bilobella* was most numerous in forests, reaching high densities (10–50% of ramets damaged) for several years in succession in certain hillside woods characterized by abundant *S. caesia* and other hosts. Such densities are exceptional for goldenrod- and aster-feeding *Dichomeris*: spring populations of all species combined in large fields rarely averaged more than one larva per 10 ramets (Root and Cappuccino, 1992). *Dichomeris bilobella* also was abundant spottily along some field margins, but it was rare in large fields.

The most common species in large and contiguous fields were *D. flavocostella* in eastern Pennsylvania and Florida, and *D. leuconotella* from northern Pennsylvania northward. With rare exceptions, I found neither of these species in forests or small forest openings; nor did R. A. Hamilton, who sampled forest and field goldenrods extensively in central New York during the same years (1989 and pers. commun.).

A fourth species, *D. levisella*, occurred fairly consistently in isolated forest openings as well as fields, but never within the forest proper. Balduf (1969) collected large numbers of *D. levisella* in northeastern Minnesota on *Aster macrophyllus*, which he reported as favoring "open places on high ground, such as clearings and roadways through woodlands."

A fifth species, *D. ochripalpella*, was evenly distributed among forest and large or small field habitats; except that it was extremely rare on the common forest goldenrod *S. caesia*, and hence was restricted to areas containing other host species.

The remaining six species were collected in open habitats. Among them, *D. non-strigella* showed great regional variation in abundance: large populations inhabited certain Massachusetts and Pennsylvania fields and roadsides (areas 3 and 4c of Fig.

Table 1. *Dichomeris* species collected at localities in Figures 1 and 2. Sampling efforts concentrated on *Solidago* species, especially *S. altissima*, *S. rugosa*, and *S. caesia*. Records are based on my rearings of caterpillars to adulthood except in the following cases: ¹Records based on larval identifications; collected caterpillars failed to reach adulthood. (Question marks in the table reflect probable but not certain larval identifications.) ²Records based on collections and rearings to adulthood by R. H. Hamilton (1989 and pers. comm.), who sampled insects extensively on *S. altissima*, *S. rugosa*, *S. bicolor* L., *S. flexicaulis* L., and *E. graminifolia*. ³Collected as pupa in leaf fold; no other likely hosts nearby.

Common species	Localities	Habitats	Host plants
1. <i>Dichomeris bilobella</i> (Zeller)	1, 2, 3, 4, 5	large and small fields, isolated forest openings, and forests	<i>Solidago altissima</i> , <i>S. arguta</i> , Ait., <i>S. bicolor</i> ^{1,2} , <i>S. caesia</i> , <i>S. canadensis</i> L. ¹ , <i>S. flexicaulis</i> , <i>S. gigantea</i> , <i>S. juncea</i> , <i>S. nemoralis</i> Ait., <i>S. rugosa</i> , <i>Aster cordifolius</i> L., <i>A. divaricatus</i> L., <i>A. lateriflorus</i> , <i>A. macrophyllus</i> L., <i>A. lanceolatus</i> Willd., <i>A. undulatus</i> L.
2. <i>D. flavocostella</i> (Clemens)	1?, 2, 3, 4?, 5, 6	large or contiguous fields	<i>S. altissima</i> , <i>S. arguta</i> , <i>S. bicolor</i> ² , <i>S. juncea</i> ? ¹ , <i>S. rugosa</i> , <i>A. novae-angliae</i> L., <i>A. lanceolatus</i>
3. <i>D. leuconotella</i> (Busck)	1, 2, 3, 4, 5	large or contiguous fields	<i>S. altissima</i> , <i>S. bicolor</i> ? ¹ , <i>S. caesia</i> ² , <i>S. gigantea</i> , <i>S. juncea</i> , <i>S. rugosa</i> , <i>Euthamia graminifolia</i> , <i>A. novae-angliae</i> ¹ , <i>A. sagittifolius</i> Wedemeyer
4. <i>D. levisella</i> (Fyles)	1?, 2, 3, 4, 5?	large and small fields including isolated openings in forests	<i>S. altissima</i> , <i>S. gigantea</i> ¹ , <i>S. rugosa</i> , <i>E. graminifolia</i> ¹ , <i>A. lanceolatus</i> ¹
5. <i>D. ochripalpella</i> (Zeller)	1, 2, 3, 4, 5	large and small fields, isolated forest openings, and forests	<i>S. altissima</i> , <i>S. bicolor</i> ² , <i>S. caesia</i> ² , <i>S. flexicaulis</i> ² , <i>S. gigantea</i> , <i>S. juncea</i> ¹ , <i>S. patula</i> Muhl., <i>S. rugosa</i> , <i>E. graminifolia</i> ^{1,2} , <i>A. cordifolius</i> ¹ , <i>A. divaricatus</i> , <i>A. lateriflorus</i> , <i>A. novae-angliae</i> , <i>A. prenanthoides</i> Muhl., <i>A. sagittifolius</i> , <i>A. lanceolatus</i> , <i>A. undulatus</i>
Rare species			
6. <i>D. inserrata</i> (Walsingham)	2, 5, 6	large fields	<i>S. altissima</i>
7. <i>D. nonsrigella</i> (Chambers)	2, 3, 4	large field, roadside, small forest opening	<i>S. altissima</i> , <i>S. gigantea</i> , <i>S. rugosa</i>

Table 1. Continued.

	Localities	Habitats	Host plants
8. <i>D. purpureofusca</i> (Walsingham)	1, 2	large fields, small opening near large fields	<i>S. altissima</i>
Species encountered only in one locality, not in central NY			
9. <i>D. achne</i> Hodges	7	on isolated patches of <i>Solidago</i> in open scrub	<i>S. fistulosa</i> Miller
10. <i>D. agonia</i> Hodges	5	dry open roadside	<i>S. juncea</i> , <i>S. nemoralis</i>
11. <i>D. juncidella</i> (Clemens)	1	large field	<i>S. gigantea</i> ³

Table 2. Additional host records, from Hodges, 1986, for the *Dichomeris* spp. collected in this study. Records duplicating those in Table 1 are omitted except when the record in Table 1 was not based on rearings from larva to adulthood.

Caterpillar species	Host plants
<i>D. leuconotella</i>	<i>Solidago uliginosa</i> Nuttall, <i>Helianthus grosseserratus</i> M. Martens
<i>D. levisella</i>	<i>Aster macrophyllus</i> , <i>A. cordifolius</i> , <i>A. lanceolatus</i> , <i>Hieracium aurantiacium</i> L.
<i>D. nonstrigella</i>	<i>Aster shortii</i> Lindley
<i>D. ochripalpella</i>	"composites"
<i>D. agonia</i>	<i>Aster</i> sp., <i>Oenothera</i> sp.
<i>D. juncidella</i>	<i>Solidago</i> sp., <i>Aster</i> sp., <i>Ambrosia artemisiifolia</i> L., <i>Artemisia trifida</i> L., <i>Helianthus tuberosus</i> L., <i>Aralia spinosa</i> L., "strawberry"

1), but I encountered only one individual in the Cayuga Lake Basin samples and none in other regions.

Gravel bars, a potentially important goldenrod habitat before forests were opened by man, were inhabited by all of the common summer-hatching species (*D. flavocostella*, *D. leuconotella*, *D. levisella*, and *D. ochripalpella*). Early instar caterpillars overwintered successfully in fair numbers on the two bars to which I transplanted them in the fall of 1984, despite the sparseness of leaf litter. The latter two bars were however spared from floods and ice scouring that winter, leaving open the possibility that gravel bars might have to be recolonized by moths that developed on host plants well up on the streambank or in more distant areas after years of exceptionally harsh physical conditions.

Many of the host plant records in Table 1 are new. Additional host records from museum specimens and the literature are summarized in Table 2, including records of plants other than *Solidago*, *Aster*, and *Euthamia*. I found that larvae could be switched from one aster or goldenrod species to another; in particular, larvae collected on asters fed readily on goldenrod, and vice versa. [Controlled experiments might detect depressions in growth rate or survival on certain host species; for example, early instar *D. leuconotella* larvae had poor survival and growth on *S. caesia* (Loeffler, 1992).]

Phenology. In the Northeast, *Dichomeris* species showed three phenological patterns (Fig. 3). Moths of four of the five common species (*D. flavocostella*, *D. leuconotella*, *D. levisella*, and *D. ochripalpella*) eclosed in late June in central New York. Judging from laboratory matings, they laid eggs through July and possibly into August. The eggs, which were laid singly on leaf undersides, hatched in as little as six days into 1 mm long larvae. These larvae grew slowly to 3–4 or occasionally 5 mm (second to fourth instars) before leaving the plants in October to overwinter in the leaf litter. By mid-November, larvae emerged in Tulgren funnels only from ground litter samples, not from equal-weight samples of leaves on standing ramets.

In late April or early May in central New York, shortly after the emergence of new ramets, the larvae crawled up the plants and resumed feeding. Further growth was rapid; final instars began appearing as early as late May in warm years, and pupae appeared by early to mid-June (Fig. 3). Pupal development lasted about two weeks. The peak of adult eclosion for all four species was in late June and early July.

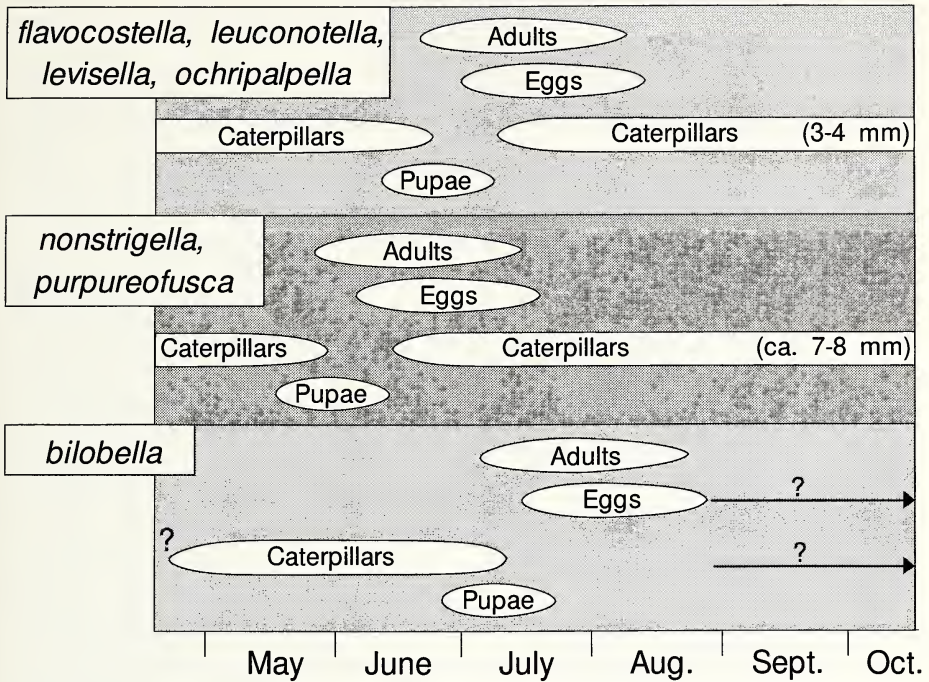


Fig. 3. Phenology of leaf-folding *Dichomeris* species on *Solidago* in central New York.

Moths of two less common species, *D. nonstrigella* and *D. purpureofusca*, flew on average approximately three weeks earlier, in June (Fig. 3). The life cycle was otherwise similar to that of the four species discussed above, except that larvae overwintered in their penultimate instar, at >6 mm in length as indicated by fall and spring collections. Final instars were found in early to mid-May. *Dichomeris agonia*, collected only in Pennsylvania, apparently follows a similar life cycle because larvae collected in early May were considerably larger than those of the first group of four species in the same locality.

Moths of *D. bilobella* appeared latest, in July (Fig. 3). In the field, I search extensively but did not find young larvae in fall, even in an abundant population at area e (Fig. 2). Only two larvae hatched on plants exposed to adults in the laboratory, from unknown egg locations (unlike the other species, captive *D. bilobella* did not oviposit on the undersides of leaves). In late April and early May, I found 2–3 mm larvae (probably second instars) in large numbers, both in the field and on laboratory oviposition plants overwintered outdoors. The *D. bilobella* larvae were considerably smaller at this time than were the larvae of other species. They reached their final instar by mid to late June.

Larvae descriptions and development. Final instar larvae of eight species can be distinguished by the following key and by Figure 4 (the remaining species are discussed below). Leaf-folding behavior is included because it is one of the most reliable diagnostic characters.

KEY TO GOLDENROD-FEEDING *DICHOMERIS* LARVAE OF
NEW YORK AND NEIGHBORING STATES

- 1a. Ground color dark chocolate brown; stripes brownish black; white spots on both meso- and metathorax; body slightly spindle-shaped, head capsule small; leaf folds loose (Fig. 7) *D. purpureofusca*
- 1b. Ground color pale to dark green; stripes green or brown; other traits variable 2
- 2a. Two mesothoracic and two metathoracic tubercles much enlarged, black; white spots on both meso- and metathorax; thorax brown. Seven stripes (the two lateroventral stripes are not visible in the dorsolateral view shown); stripes greenish-brown, broad, even; body slightly spindle-shaped, head capsule small; leaf folds loose (Fig. 7) *D. nonstrigella*
- 2b. No tubercles enlarged; mesothorax black; metathorax black with white patches on posterior third; abdomen stripeless or with five green or brown stripes; body relatively linear; leaf folds variable 3
- 3a. Abdomen pea green and stripeless, except for a dorsal dark-green line (apparently reflecting the internal contents of the caterpillar rather than the distribution of pigment); tubercles easily seen; leaf folds loose (Fig. 7) *D. agonia*
- 3b. Abdomen pale green (whitish in molting specimens), with darker, green or brown stripes; other traits variable 4
- 4a. Stripes medium dark greenish brown to dark brown; lateral stripes extend to tip of abdomen, forming a V; tubercles generally difficult to see against stripes; leaf folds loose (Fig. 7) 5
- 4b. Stripes light to medium green or brownish green (light brown in molting specimens); other traits variable 6
- 5a. Stripes medium dark greenish brown, broad, and even; anal V near-black and exceptionally broad; largest species (up to 18 mm) *D. flavocostella*
- 5b. Stripes dark watery brown; dorsal stripe usually narrow and faded, particularly at anterior end; anal V of same shade as stripes, less broad than in *D. flavocostella* (Note: some individuals overlap in characteristics with *D. flavocostella* and cannot be reliably distinguished until they reach adulthood) *D. leuconotella*
- 6a. Lateral stripes greenish, not darkened on metathorax; lateral stripes extend only to middle of terminal abdominal segment; tubercles easily seen; smallest species (larva up to 15 mm); leaf folds tight (Fig. 7) *D. ochripalpella*
- 6b. Lower portions of lateral stripes nearly black on metathorax; other traits variable ... 7
- 7a. Anal V dark brown; stripes pea-green; tubercles easily seen, surrounded by pale green rings; leaf folds tight (Fig. 7) *D. bilobella*
- 7b. Anal V medium green and obscure; stripes medium green, slightly lighter than those of *D. bilobella*; tubercles blend with stripes and are difficult to see; leaf folds loose (Fig. 7) *D. levisella*

Among the remaining three species collected in this study, larvae of *D. inserrata* lack stripes altogether and, unlike the other species, inhabit the terminal bud throughout their development rather than folded leaves. They are light green with relatively round black heads and thoracic shields. I have not seen larvae of *D. juncidella*; a description by Murtfeldt (1874) (as *Depressaria dubitella*) suggested that they are similar in overall pattern to *D. bilobella* and *D. ochripalpella*. The larvae of *D. achne* that I examined in south-central Florida closely resembled those of *D. ochripalpella*.

Lengths of full-grown larvae differed among the species, being approximately 16–18 mm for *D. flavocostella*, 15–17 mm for *D. bilobella*, *D. leuconotella*, and *D. levisella*, and 13.5–15.5 mm for *D. ochripalpella*, *D. nonstrigella*, and *D. purpureofusca*.

Larvae of *D. leuconotella*, the species that I monitored most closely, appeared to go through six instars when reared indoors. Also, preserved specimens sorted into six classes of head capsule size. But observations of newly emerged individuals in spring, thought to be third instars, suggested that some individuals pass through an extra molt with relatively little change in head capsule width while at overwintering size (3–5 mm). Thus, some proportion of the population may pass through seven instars. Molts tended to occur at body lengths of 1.5–2.0 mm, 2.5–3.0 mm, 3.5–4.5 mm, 6–7 mm, and 10–12 mm. Caterpillars of the other *Dichomeris* species also typically molted at these lengths.

Early-instar larvae are not easily identified to species. Among the species I bred (all those in Fig. 4 except *D. agonia*), first instars are 1–2 mm long and pale green with yellow heads and shields that darken through brown to black by the third instar, with some variation among species in rate of darkening. All develop stripes on the mesothorax in the late second or third instar; abdominal stripes appear and gradually darken during the third instar (or the fifth in *D. bilobella*). *Dichomeris nonstrigella* and *D. purpureofusca* caterpillars are distinguished from the third instar onward by an extra row of white spots on the metathorax, which are distinctive for each species (Fig. 4). The characteristic thoracic spikes of *D. nonstrigella* develop at variable rates over the third through fifth instars, and *D. purpureofusca* larvae gradually darken from green to nearly black over those same stages. Subtle differences distinguishing third, fourth, and fifth instars of the four common summer-hatching species (*D. flavocostella*, *D. leuconotella*, *D. levisella*, and *D. ochripalpella*) are described in Loeffler (1992); briefly, *D. flavocostella* stripes are uniform in width and the anal V becomes broad and dark during the third or fourth instar; *D. leuconotella* larvae have a narrow, faded or broken dorsal stripe and an anal V that is usually no darker and sometimes lighter than the rest of the stripes; and *D. levisella* stripes are relatively light in shade, except on the metathorax where the lateral stripes become dark brown. Third and fourth instar *D. ochripalpella* larvae are variable and intermediate among the other three species in all of these respects but are distinctive for the abrupt termination of all five stripes in the middle of the 10th abdominal segment, with only a thin shadow of an anal V continuing to the tip of the abdomen. The five stripes lighten to brownish-green or medium green (like those of *D. levisella*) after the molt to the fifth instar, at about 6–7 mm.

Excellent keys, descriptions, and photographs of adults of the 11 species have been given by Hodges (1986). Live adult weights of some well-fed specimens corresponded well to the relative final lengths of larvae of the species, being 10–14 mg for the large species *D. flavocostella* (N = 4 males, 5 females), 9–12 mg for *D. bilobella* (N = 6 males, 2 females), 8–13 mg for *D. leuconotella* (N = 5 males, 3 females), 8–12 mg for *D. levisella* (N = 5 males, 2 females), and 5–10 mg for the small species *D. ochripalpella* (N = 8 males, 11 females).

Larval behavior. Newly hatched caterpillars were too small to fold leaves, and those of summer-hatching species typically moved into whatever cracks or crannies were available near their hatch sites on the leaf undersides. Most larvae aligned themselves in the angle between a leaf midrib and the lower surface of the blade, although some moved into shelters created by other insects: between the clustered leaves of rosette galls (*Rhopalomyia* spp., Diptera: Cecidomyiidae) and button galls (*Asphondylia* sp., Diptera: Cecidomyiidae), inside the leaf mines of caterpillars of *Cremastobombycia solidaginis* (Lepidoptera: Gracillariidae), in leaf ties of other Lepidoptera such as *Herpetogramma* spp. (Pyralidae) and *Phaneta formosana* (Tortricidae), or even in old leaf folds of the previous generation of *Dichomeris*. The larvae spun a silk mat and rested beneath it, protected from predators by the silk and by their immobility (Loeffler, 1992). They fed in short bouts, creating small pits both beneath the mat and within a few millimeters of the opening at either end (Fig. 5a). Larvae of *D. nonstrigella* formed unusually long mats, virtual tunnels extending for many millimeters along the midribs and frequently branching to follow side veins (Fig. 5b). In all species, the addition of silk gradually caused the leaf to crinkle and fold over the mat (Fig. 5c), at a rate depending on the host species and the size and age of the leaf. Folded leaves provide a larger surface area for feeding within the protection of the refuge. Among caterpillars of the four common summer-hatching species (uppermost in Fig. 4), many

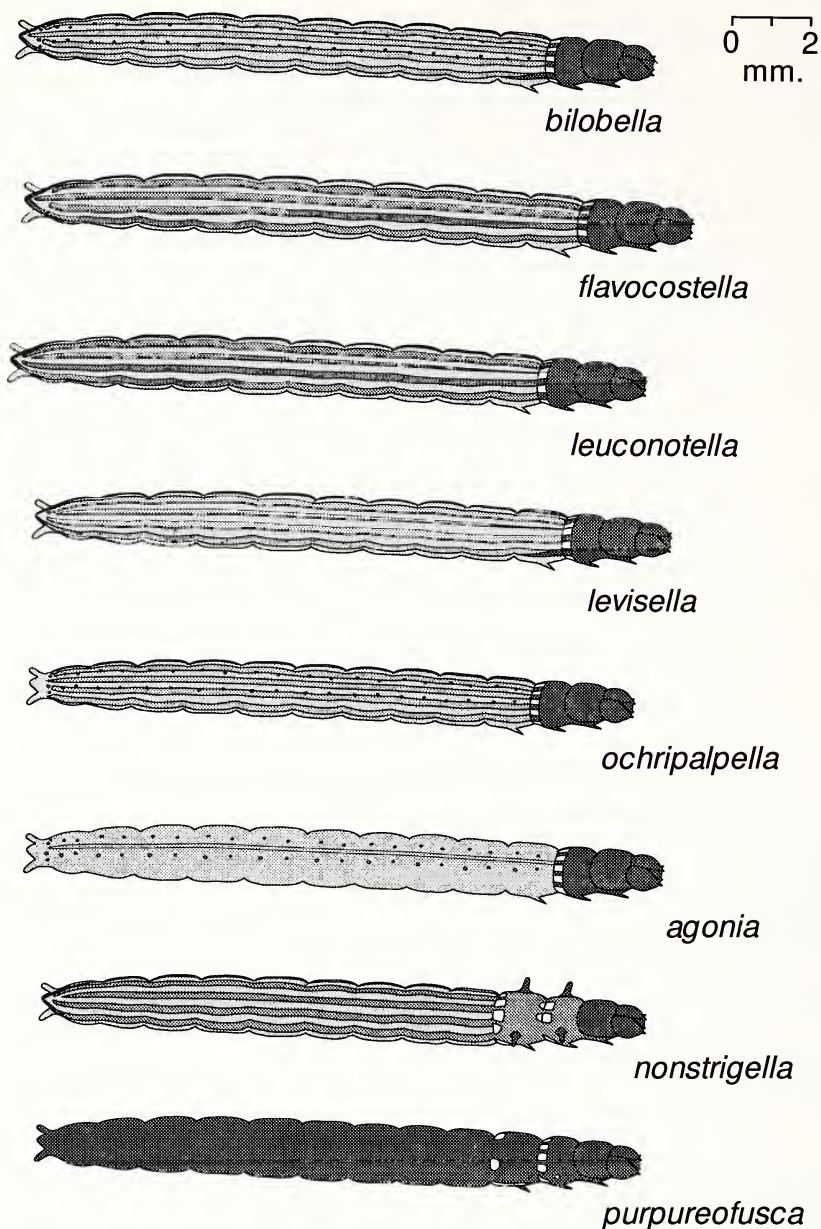


Fig. 4. Patterns and other diagnostic features of goldenrod-feeding *Dichomeris* caterpillars (dorsolateral views of final instars) in New York and neighboring states. For a key to final instars and for descriptions of younger larvae, see text. In all species, head capsules and prothoracic shields are black.

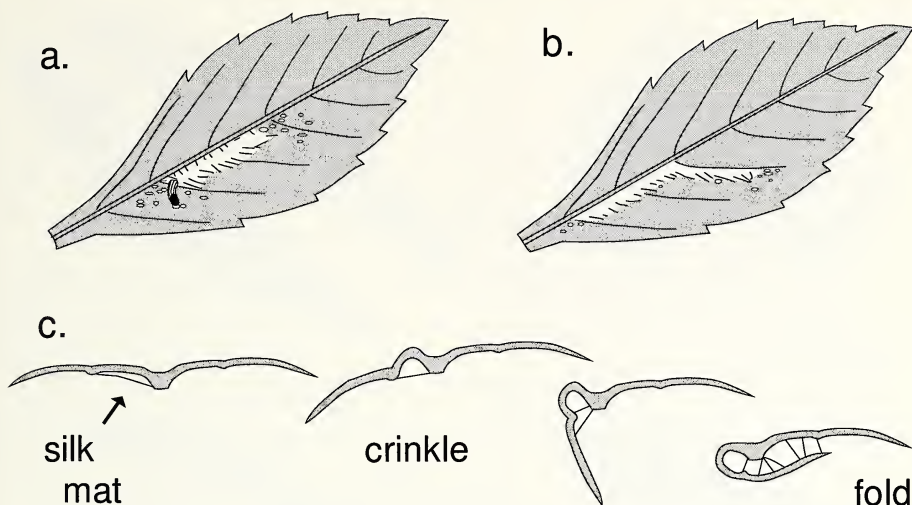


FIG. 5. Refuges of young leaf-folding *Dichomeris* larvae. a) Silk mat and feeding pits characteristic of most summer-hatching species. b) Longer silk tunnels characteristic of *D. non-strigella*. c) Leaf cross sections showing how, by adding silk over a period of days or weeks, a caterpillar crinkles and eventually folds a leaf.

individuals remained in a single refuge for most of the late summer and fall; others left their refuges and constructed new ones several times over that period.

In October, caterpillars reared outdoors on excised leaves frequently left their refuges and crawled throughout the rearing vial, especially as the conditions of the leaves supplied to them deteriorated. Such wanderings presumably corresponded to the emigration of wild larvae from the senescing plants to the ground litter. These caterpillars eventually settled on senesced leaves and formed winter refuges consisting of short folds sealed at either end. The larvae formed similar sealed refuges in pieces of paper towel, when those were available. They remained in these shelters until spring. Although larvae generally ranged in length from 3 to 5 mm at this time, they were capable of overwintering at larger sizes; I successfully overwintered captive larvae outdoors at lengths of 3–9 mm.

The slow development of young larvae in late summer was apparently enforced primarily by environmental factors and secondarily by genetic factors that varied among larvae. Young larvae reared at constant room temperature on fresh foliage responded differentially: some individuals of each species grew to adulthood without interruption while others grew extremely slowly or halted growth altogether for several months while in the 5–7 mm range. I maintained a continuously breeding indoor colony of *D. leuconotella* from summer of 1986 to summer of 1988, in which many individuals completed development from egg to adulthood in about three months.

In experiments addressing how far overwintering larvae strayed from their autumnal host, I found that some overwintering *D. leuconotella* and *D. flavocostella* larvae (3–5 mm in size) stayed within a few cm of their host and reascended it, or perhaps an immediate neighbor, in spring. Others however moved through the litter up to 30 cm or more between October and April. Thus, in diverse fields, larvae have opportunity to ascend hosts of different species than their fall ramets.

To study the caterpillars' behavior on a range of hosts of varied leaf morphology, I supplemented field observations with close monitoring of 14 field-reared *D. leuconotella* and *D. levisella*

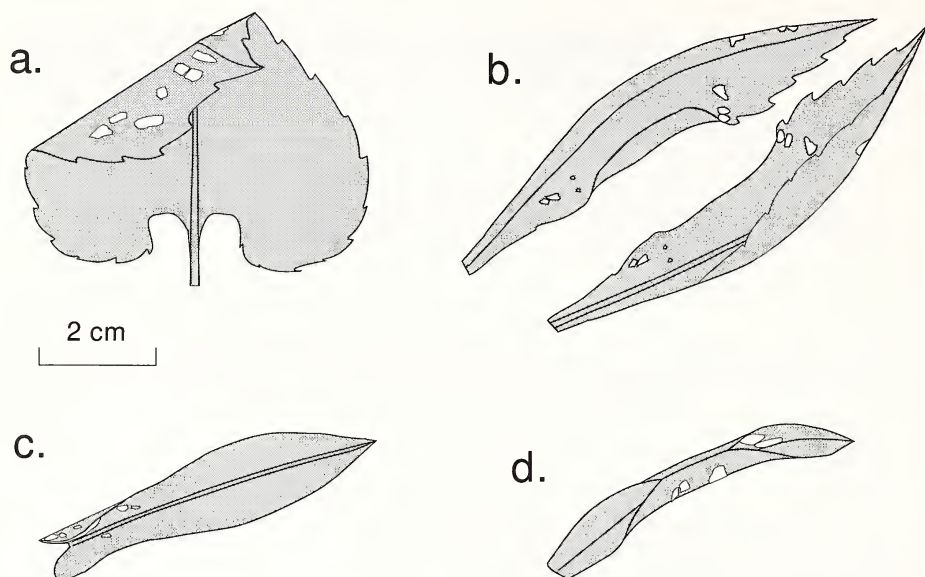


Fig. 6. A representative sample of the refuges formed on different species of *Solidago* and *Aster* by early-to-middle-instar *D. leuconotella* and *D. levisella* larvae on spring rosettes. a) Exceptionally broad leaves such as those of *Aster cordifolius* were sometimes folded approximately transversely rather than lengthwise. b) On thin-leaved forest goldenrods (*S. caesia*, *S. arguta*, *S. flexicaulis*), larvae typically first colonized the naturally upwardly-curved margin of a leaf that had not yet expanded from the terminal bud. Shown here are upper and lower sides of a leaf of *S. caesia*, with the larva's first refuge on the upper side, and with a later, larger fold constructed on the lower surface after the leaf had unfolded and assumed the downward flare characteristic of many leaves on these species. c) On leaves with downwardly bent auricles, as in the *Aster novae-angliae* leaf shown (viewed from below), or with strongly declinate wings running the length of the petioles as in *A. novi-belgii* or *A. prenanthoides*, the caterpillar formed a web and eventually a fold on the lower side, in the curl of the flange or wing. d) Narrow leaves of *Euthamia graminifolia* or *A. pilosus* were folded in half from the midrib, upward or downward depending on which way the leaves were naturally curved.

larvae on potted plants of 14 different species of *Solidago*, *Euthamia*, and *Aster* in early April of 1986. Larvae always sought out cracks or curves in the leaves that gave them a head start in constructing a refuge. Because the deepest cracks and curves varied in location among the host species, the larvae spun refuges that likewise varied in location and overall form depending on the nature of the host (Fig. 6, and see Loeffler, 1992).

Caterpillars made several refuges in spring, most of them during the final instar. Feeding damage began as pits, less than 1 mm^2 in size, which did not puncture the leaf but left the opposite surface layer intact (Fig. 6). Feeding occurred several times per day, both in light and in dark (this was tested by examining plants immediately before and after placement in a closed cupboard at night). Each feeding bout lasted a few minutes. By the time the caterpillar was 6–7 mm in length and had molted to its penultimate instar, the pits were 1–2 mm wide and up to several mm long regardless of host species. Shortly thereafter, the larva typically began making indentations from the leaf margin, at either end of its refuge. Final instars ($> 10 \text{ mm}$)

*D. leuconotella**D. bilobella*

4th instars

6th instars

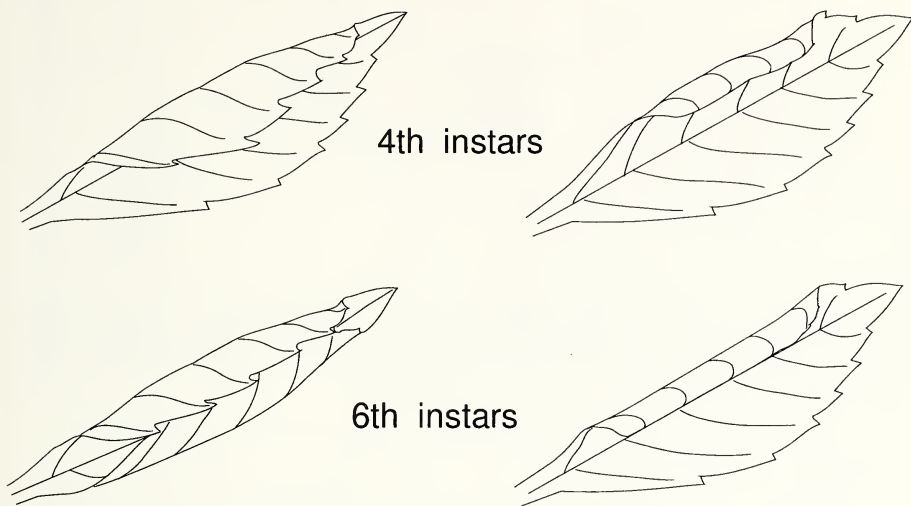


Fig. 7. Comparison of "loose" leaf folds of older caterpillars of *D. leuconotella* with "tight" leaf folds of *D. bilobella* (drawings copied from sketches of representative leaf folds). Other loose-folding species are *D. flavocostella*, *D. levisella*, *D. nonstrigella*, and *D. purpureofusca*; other tight-folding species are *D. ochripalpella* and *D. achne*.

sometimes still pitted the leaf, but they more typically chewed indentations in the margin, outside either end of the leaf fold. They also fed on adjacent leaves, which they reached by stretching between leaves or by actually wandering a cm or two up the stem. Refuges were abandoned as they became mangled, and new ones were typically built on higher leaves, so that the caterpillar stayed within the upper or upper-middle leaves of the plant as it grew. Regardless of host species, the larvae constructed a relatively narrow fold in which to pupate.

Larvae of *D. bilobella*, which did not appear until the spring following egg laying, had similar behavior to those of summer-hatching species except that early instars did not form mats on the undersides of leaves. Rather, they fed between leaves of the terminal bud, soon forming folds along the margins of terminal leaves expanding from the bud. Such behavior was possible because the leaves in the terminal buds of goldenrods and asters are large and pliable in spring; they are small or lacking by late summer.

Caterpillars of three species—*D. bilobella*, *D. ochripalpella*, and *D. achne*—characteristically folded leaves much more tightly than the others (Fig. 7). Their feeding damage consisted mainly of pits and indentations in the leaf margin outside either end of the fold (Fig. 8).

Adult behavior and host plant choice. Captive adults of the common goldenrod-feeding *Dichomeris* species were nocturnal; individuals that I monitored closely for 24 hours or more moved about chiefly after dark, and most of the times that I observed mating or feeding were at night.

The moths fed both on pieces of fruit and on dilute solutions of honey or boiled honey and fruit supplied in cotton or tissue. Although I rarely observed feeding, adult longevity (40–50 days or more for many individuals of both sexes) suggested that feeding is important. Egg production was much greater in small rearing boxes, where the moths were always in close proximity to food, than in large cages.

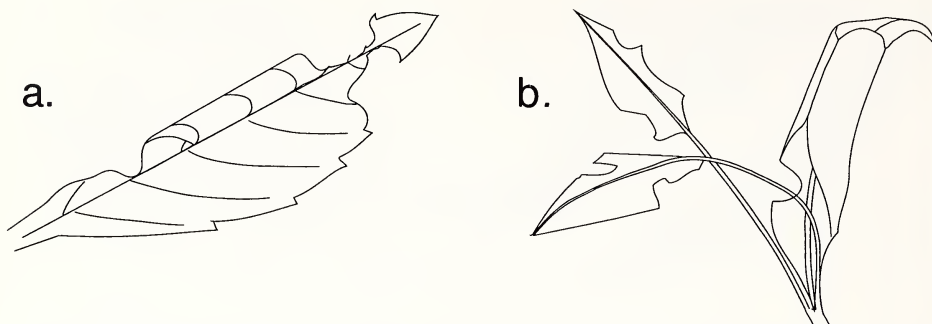


Fig. 8. Leaf-chewing damage of final instars of a) *D. bilobella*, a tight-folding species and b) *D. leuconotella*, a loose-folding species. Larvae of both tight- and loose-folding species frequently ventured one or two body-lengths from their refuges to chew on adjacent leaves. Goldenrod species shown are a) *S. rugosa* and b) *S. gigantea*.

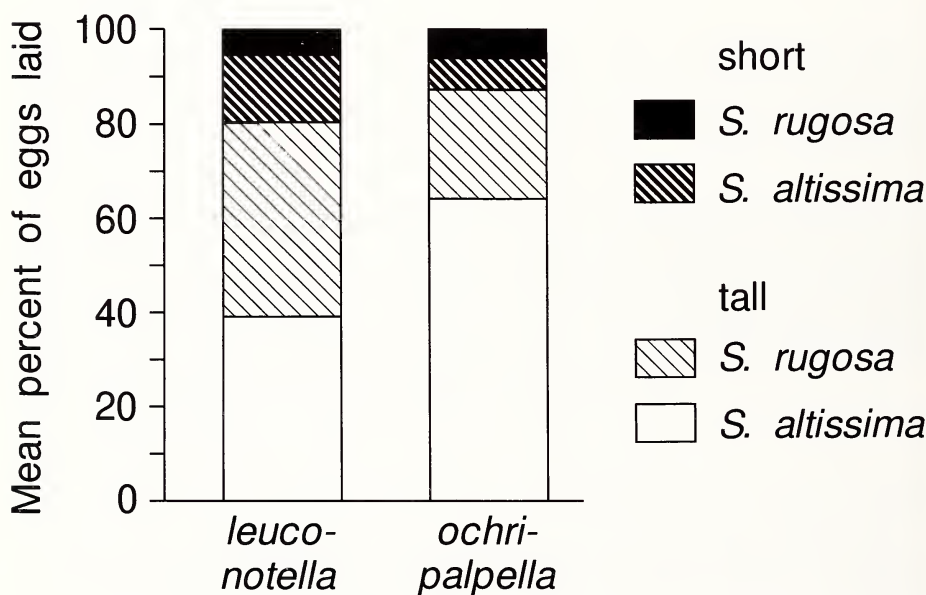


Fig. 9. Results of 12 exposures of groups of *D. leuconotella* moths and 4 exposures of groups of *D. ochripalpella* moths to tall (28 cm) and short (14 cm) sprigs of two common field goldenrods. For *D. leuconotella*, differences in preference among the four types of sprigs were significant (Quade test, $T_1 = 7.75$, $df = 3,33$, $P < 0.01$), with followup comparisons indicating significant preference for tall ramets of either species over short ramets of either species, but no significant preference between *S. altissima* and *S. rugosa*. Results for *D. ochripalpella* were marginally nonsignificant (Quade Test, $T_1 = 3.14$, $df = 3,9$, $0.05 < P < 0.10$), probably because of small sample size. If moths lay eggs singly rather than in close succession, then a goodness of fit G test reveals highly significant results ($P < 0.001$) for *D. ochripalpella*.

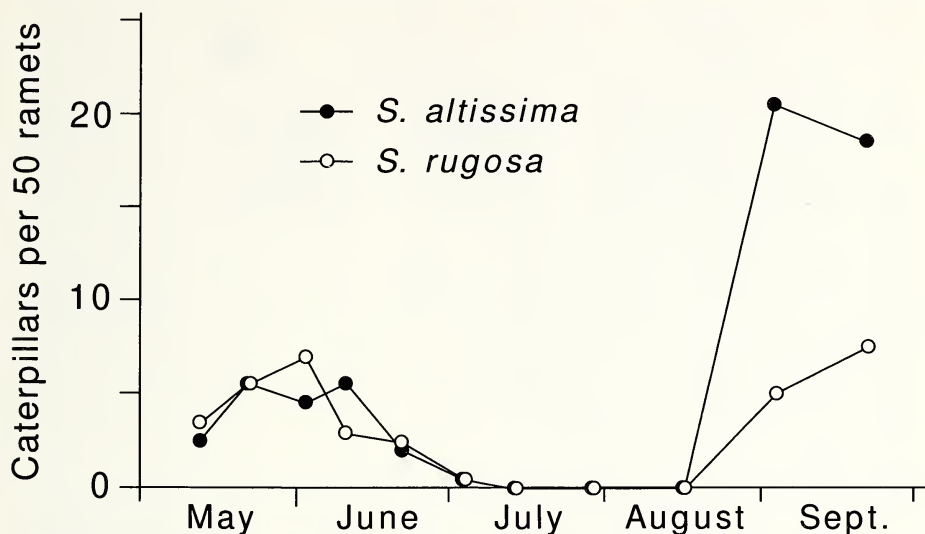


Fig. 10. Number of *Dichomeris* caterpillars (combined species) per 50 stems of *Solidago altissima* or *S. rugosa*, averaged for two fields (areas b and c, Figure 2) sampled in 1984.

Females mated and began laying eggs within a week of eclosion. I usually kept moths in groups and did not attempt to quantify egg production per individual, but a *D. purpureofusca* female laid a total of more than 200 eggs over five weeks, and a *D. flavocostella* female laid 87 eggs over two days following three nights of mating activity. Production for most females was highest within the first two weeks following eclosion, although egg-laying generally continued throughout most of their adult lives.

Eggs of captive females were laid on upper, middle, and lower leaves and on stems, but typically on the lower surfaces of the leaves. Females of the two species tested, *D. leuconotella* and *D. ochripalpella*, showed a preference for taller ramets (Fig. 9). Such a preference has consequences for distribution of eggs among host species: *S. altissima* is the taller of the two common field goldenrods (Root, Loeffler, and Rawlins, unpubl.), and harbored a significantly greater abundance of late-summer larvae than did the shorter species *S. rugosa* in two fields in which these hosts grew intermingled (Fig. 10). In spring the larvae distribution on *S. altissima* and *S. rugosa* was more even (Fig. 10), presumably because the overwintered larvae encountered and ascended ramets indiscriminately.

Adults also had preferences among host species irrespective of size. *Dichomeris leuconotella*, *D. ochripalpella*, *D. flavocostella*, and *D. levisella* all laid more eggs on ramet tops of *S. rugosa*, especially field-grown plants, than on ramet tops of *S. caesia* (Fig. 11); although small numbers of trials (because of limited supplies of adults) constrained the statistical interpretations of the data for the latter two species (Fig. 11). Informal observations suggested that differences existed among several other host species as well, with *S. altissima* being perhaps the preferred host.

Parasitoids. Nineteen species of wasps in four families and one species of tachinid fly parasitized *Dichomeris* specimens in my collections, and three additional species of wasps occurred as hyperparasites (Table 3). Most of these parasitoids are polyphagous, attacking lepidopterous larvae or pupae of more than one family (Krombein et al., 1979). The frequent parasitoid *Isomeris marginata* may however specialize on *Dichomeris*; the only previous rearings were from *Dichomeris levisella* (as *Pimpla marginata*; Balduf, 1969). No other parasitoids in

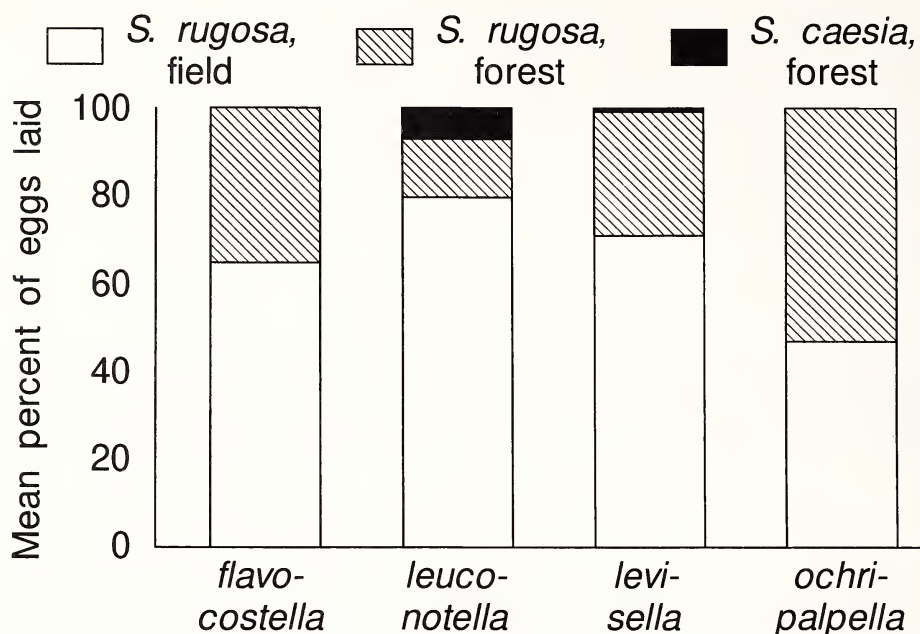


Fig. 11. Results of exposures of groups of *D. leuconotella* (leuco, 15 trials), *D. ochripalpella* (ochri, eight trials), *D. flavocostella* (flavo, four trials), and *D. levisella* (levi, three trials) moths to sprigs of field and forest goldenrods. The first two species showed significant preference for *S. rugosa*, especially field-grown stems; the forest species *S. caesia* received almost no eggs. (Quade test for *D. leuconotella*: $T_1 = 17.201$, $df = 2,28$, $P < 0.01$; followup comparisons indicated significant preferences for field *S. rugosa* over forest *S. rugosa* and for forest *S. rugosa* over *S. caesia*. Quade Test for *D. ochripalpella*: $T_1 = 20.577$, $df = 2,14$, $P < 0.01$; followup comparisons indicated significant preferences for field *S. rugosa* over either forest *S. rugosa* or *S. caesia* but not for forest *S. rugosa* over *S. caesia*.) *Dichomeris flavocostella* and *D. levisella* trials were too few for analysis by Quade tests, but G tests (assuming eggs to be independent events) show highly significant preferences of *S. rugosa* in both cases ($P < 0.001$).

Table 3 have been previously reported from goldenrod-feeding *Dichomeris* species except the hyperparasite *Dimmockia pallipes*, which was reared from four parasitoids of *D. levisella* by Balduf (1969). Some closely related parasitoids have however been reared from goldenrod-feeding *Dichomeris*: *Paralitomastix pyralidis* (Ashmead) from *D. flavocostella* (Krombein et al., 1979), and *Meteorus dimidiatus* (Cresson), *Oncophanes pusillus* Muesebeck, *Orgillus indigator* Muesebeck, *Pediobius sexdentatus* (Girault), *Temelucha* sp. near *epagoges*, and *Campoplex* sp. from *D. levisella* (Balduf, 1969).

The reared *Isomeris marginata* in this study were all females. They emerged from fully grown caterpillars and spun a cylindrical brown cocoon, inside the tight leaf fold in which the host larva would have pupated. They closed both ends of the leaf fold (pupating *Dichomeris* larvae left the fold open at their anterior end). I reared some specimens from young larvae collected in late summer, which indicated that *I. marginata* oviposits in early instar caterpillars, and developing parasitoids overwinter inside the host larvae. Balduf (1969) gives further details on the biology and natural history of this parasitoid.

The common braconids (all three *Apanteles* spp., *Meteorus* sp., and *Orgillus consuetus*) also attacked in summer and overwintered in the host, but all emerged from *Dichomeris* caterpillars that were half to three-quarters grown. *Apanteles* spp. and *O. consuetus* greatly slowed the growth of the caterpillars, such that cocoons often did not appear in the leaf folds until July. Caterpillars parasitized by *Meteorus* sp. grew at a close to normal rate, and cocoons appeared in leaf folds in May or early June. As with the *D. levisella* caterpillars parasitized by *Meteorus dimidiatus* in Balduf's (1969) study, caterpillars from which a *Meteorus* sp. larva had emerged did not die for several days. They typically remained in the leaf fold with the parasitoid cocoon and did not feed, but they were capable of crawling if disturbed.

Among other frequent parasites, the eulophid *Elarchertus argissa* attacked caterpillars throughout the growing season. After killing the larva, the pinkish-green grub developed externally, feeding on the cadaver in the leaf fold. This polyphagous parasite was quite small (usually <2 mm), but its size was highly variable depending on the size of the host caterpillar.

The encyrtid, *Paralitomastix* sp., was the most frequent parasite of *D. bilobella* larvae. Host larvae developed normally, but in their final instar become extremely large and swollen, with several dozen wasp larvae (as many as 81). The parasitoids pupated within the dead caterpillar skin.

The rearings in this study for the recently described tachinid, *Actia dimorpha* (O'Hara, 1991) represent the only host records to date (J. E. O'Hara, pers. comm.). Maggots emerged from final instar caterpillars, one maggot per larva, and formed small brown puparia.

Among summer-hatching *Dichomeris* species, rates of parasitism varied widely (0–100%, with the extremes encountered in smaller samples), but in large samples they were generally 40–50%. Rates appeared similar between adjacent forests and fields, on *D. ochripalpella* (e.g., 22 of 51 specimens or 43% in forests, 17 of 33 specimens or 52% in fields, in two sampling areas in 1985). There were no obvious differences in rate of parasitism among the four common summer-hatching *Dichomeris* species, and most of the parasitoid species characterized as "frequent" (Table 2) were recovered from all four species.

The spring-appearing *D. bilobella* had a separate parasitoid complex. Its chief parasite was *Paralitomastix* sp., which did not attack the summer-hatching species. Conversely, most of the parasitoids of summer-hatching species did not attack *D. bilobella* (an exception was *Actia dimorpha*). Rates of parasitism of *D. bilobella* were low, often near 0%; high rates occurred only in the dense population at Treman State Park, where 40% of *D. bilobella* larvae from a 1985 collection (N = 89) succumbed to *Paralitomastix* sp.

DISCUSSION

The present study brings to 14 the number of North American *Dichomeris* species known to feed on *Solidago* and its close relatives, with a total of 11 species reported from the northeastern United States. Additional *Dichomeris* species may well be present on these hosts; many species still lack host records and may have been missed to date because of rare or spotty distributions. Certainly the *Dichomeris* lineage is well-adapted to these hosts, given the large number of species known to use *Solidago* and *Aster* and their relative abundance among goldenrod-feeding Lepidoptera (Root, Loeffler, and Rawlins, unpubl.).

Powell (1980) pointed out that a given lepidopteran lineage may be characterized by a given level of feeding specialization. Evidence suggests that *Dichomeris* species are oligophagous, feeding on almost any species of *Solidago*, and perhaps on most species of *Aster* as well as other composites. In the laboratory, caterpillars generally accept whatever host plant species they encounter within this group, and their leaf-

Table 3. Parasitoids reared from *Dichomeris* larvae on *Solidago*, *Euthamia*, and *Aster*. Bilob = *D. bilobella*, flavo = *D. flavocostella*, leuco = *D. leuconotella*, levi = *D. levisella*, ochri = *D. ochripalpella*, nons = *D. nonstrigella*. Some caterpillars collected in early years of the study, or collected and reared in large groups to supply breeding stock, were not identified or were only identified as "*flavocostella* or *leuconotella*," if dark striped. Frequent = reared from many specimens; somewhat frequent = reared from 10-20 specimens; infrequent = reared from 3-10 specimens; rare = reared from 1-2 specimens.

<i>Dichomeris</i> species parasitized		Occurrence
Hymenoptera: Braconidae		
<i>Apanteles</i> sp. 1, prob. undescribed	ochri, levi	frequent
<i>Apanteles</i> sp. 2	not identified (mass collections)	somewhat frequent
<i>Apanteles</i> sp. 3	flavo and/or leuco, and probably levi	somewhat frequent
<i>Bracon gelechiæ</i> Ashmead	probably bilob (unidentifiable cadaver)	rare
<i>Meteorus</i> sp. possibly bakeri C.D.	flavo and/or leuco, levi, ochri, nons	frequent
<i>Meteorus hyphantriæ</i> Riley	not identified (mass collection)	rare
<i>Oncophanes</i> sp.	flavo and/or leuco, unidentifiable cadavers	infrequent
<i>Orgilus consuetus</i> Muesebeck	flavo, leuco, ochri, probably levi	frequent
Possibly <i>Rhyssipolis</i> sp.	ochri	rare
Hymenoptera: Eulophidae		
<i>Dimmockia pallipes</i> Muesebeck	unidentified wasp cocoon from leuco	hyperparasite, rare
<i>Elachertus argissa</i> (Walker)	flavo and/or leuco, ochri, levi	frequent
<i>Pediobius facialis</i> (Giraud)	unidentified pupæ	rare
Hymenoptera: Encyrtidae		
<i>Paralitomastix</i> sp.	bilob	frequent
Ichneumonidae		
<i>Campoplex</i> sp.	flavo and/or leuco, ochri	somewhat frequent
<i>Coccygominus aequalis</i> (Prov.) or <i>annulipes</i> (Brulle)	leuco	rare
<i>Diadegma</i> sp. (one or two spp.)	bilob, flavo or leuco	rare
<i>Exochus decoratus acitulus</i> Prov.	bilob	rare
<i>Isomeris marginata</i> (Prov.)	flavo, leuco, ochri, and levi	frequent

Table 3. Continued.

Dichomeris species parasitized		Occurrence
<i>Itoplectis conquisitor</i> (Say)	cocoons of <i>Isomeris marginata</i> and unidentified braconids	hyperparasite, infrequent
<i>Mesochorus vittator</i> (Zett.)	cocoon of <i>Isomeris marginata</i>	hyperparasite, rare
<i>Temelucha platynotae</i> (Cush.)	flavo and/or leuco, ochri, nons	infrequent, specimens mostly from eastern PA
<i>Trichstus chosis</i> Tow.	flavo and/or leuco, nons, unidentified pupae	infrequent
Diptera: Tachinidae		
<i>Actia dimorpha</i> O'Hara	bilob, flavo, leuco	frequent

folding behavior is flexible enough to allow them to use this moderately diverse array of hosts efficiently. Adults show more discrimination than larvae [a logical correlate of their greater mobility, also documented by Messina (1982) for the goldenrod-feeding chrysomelid beetle *Trirabda virgata*]. Consequently, distributions of larvae among host plant species in late summer, when adults choose the plants, differ from distributions in the following spring when the choice is made by larvae. In some cases (e.g., between *S. altissima* and *S. rugosa*), adult discrimination is based more on plant size than on plant species; but the avoidance of *S. caesia* by adults is striking; only *D. bilobella* regularly uses *S. caesia* as a host.

The *Dichomeris* species known to feed on goldenrods do not form a monophyletic lineage. Most such species are members of the large *setosella* species-group, but they are not closely allied within that group based on adult characteristics (Hodges, 1986). *Dichomeris flavocostella* is the most distantly related, being placed by Hodges (1986) in a different species-group; the resemblance of its caterpillars to those of other goldenrod-feeding species in color pattern, behavior, and phenology may be interesting examples of parallelism or convergence. Indeed, closer morphological study of the caterpillars of all members of both species-groups could be revealing, particularly after the host plant affinities of more species become known. Hodges (1986) identified two species pairs among the taxa discussed here, based on adult characteristics. These were 1) *D. nonstrigella* and *D. purpureofusca*, and 2) *D. ochripalpella* and *D. achne*. Larvae of *D. purpureofusca* and *D. achne* had not been reared before the present study. The larvae within each pair do show strong resemblances: *D. nonstrigella* and *D. purpureofusca* caterpillars share advanced phenology as well as wide bodies, small head capsules, and complex thoracic spot patterns; and *D. ochripalpella* and *D. achne* caterpillars share slender builds, similar coloration, and similar behavior (both form tight marginal leaf folds).

Observations from this study point out species differences which may have ecological as well as phylogenetic significance. For example, differences in the tightness of leaf folds are potentially linked to habitat use: in the northeast, tight folds are constructed only by the forest-inhabiting *D. bilobella* and *D. ochripalpella* and not by the species restricted to open habitats. However, reasons for this putative relationship remain unclear. Exposure of caterpillars of loose-folding and tight-folding species to forest and field predators, and monitoring of larvae transplanted to field and forest plants (Loeffler, 1992), gave no indication that loose folds provide superior protection in fields or that tight folds protect better in forests.

Subtle differences in phenology among summer-hatching species correlate with species abundance. Leaf-folding species hatching in July and overwintering as third or fourth instars (*D. flavocostella*, *D. leuconotella*, *D. levisella*, and *D. ochripalpella*) were generally more widespread and common than those hatching in June and overwintering as fourth or fifth instars (*D. agonia*, *D. nonstrigella*, and *D. purpureofusca*). Any causal relationship must be based on timing rather than length of the life stages, because the stages are of similar lengths among June- and July-hatching species. Possible reasons might include improved adult reproduction, egg or larval survival, etc. later in the year.

Finally, a clear relationship was evident between parasitism and the unique phenology of *D. bilobella*. This spring species suffered relatively little parasitism and did not host most of the species that attacked summer-hatching *Dichomeris* caterpillars.

The interplay between developmental timing and parasitism could therefore play a major role in the phenological divergence of caterpillar lineages.

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